Auditory Midbrain Representation of a Break in Interaural Correlation

(Running Title: Temporal Fine Structure and Envelope)

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ABSTRACT

The auditory peripheral system filters broadband sounds into narrowband waves, and decomposes narrowband waves into quickly-varying temporal fine structures (TFSs) and slowly-varying envelopes. When a noise is presented binaurally (with the interaural correlation being 1), human listeners can detect a transient break in interaural correlation (BIC), which does not alter monaural inputs substantially. The central correlates of BIC are unknown. This study examined whether phase-locking based frequency-following responses (FFRs) of neuron populations in the rat auditory midbrain (inferior colliculus, IC) to interaurally correlated steady-state narrowband noises are modulated by introducing a BIC. The results showed that the noise-induced FFR exhibited both a TFS component ($\text{FFR}_{\text{TFS}}$) and an envelope component ($\text{FFR}_{\text{Env}}$), signaling the center frequency and bandwidth, respectively. Introducing either a BIC or an interaurally correlated amplitude-gap (which had the summated amplitude matched to the BIC) significantly reduced both $\text{FFR}_{\text{TFS}}$ and $\text{FFR}_{\text{Env}}$. However, the BIC-induced $\text{FFR}_{\text{TFS}}$ reduction and $\text{FFR}_{\text{Env}}$ reduction were not correlated with the amplitude-gap-induced $\text{FFR}_{\text{TFS}}$ reduction and $\text{FFR}_{\text{Env}}$ reduction, respectively. Thus, although introducing a BIC does not affect monaural inputs, it causes a temporary reduction in sustained responses of IC neuron populations to the noise. This BIC-induced FFR reduction is not based on a simple linear summation of noise signals.
INTRODUCTION

Interaural correlation (IAC) is defined as the similarity of sound waves presented at the two ears (Jeffress et al., 1962). The IAC-based binaural processing plays a critical role in both sound localization (Coffey et al., 2006; Franken et al., 2014; Soeta and Nakagawa, 2006) and target-object detection in noisy environments (Durlach et al., 1986; Palmer et al., 1999). The IAC also affects the auditory perception. For example, when the IAC drops from 1 to 0, without affecting the spectra of monaural inputs, the auditory image of the simultaneously-arrived binaural sounds changes vividly from a single image located at the head center into two separated images at each ear (Blauert and Lindemann, 1986; Culling et al., 2001). Accordingly, human listeners with normal hearing can easily detect an interaurally uncorrelated fragment embedded in the interaurally correlated noises (Akeroyd and Summerfield, 1999; Boehnke et al., 2002; Huang et al., 2008, 2009a,b; Kong et al., 2012, 2015; Li et al., 2009; Li et al., 2013), i.e., a transient change of IAC from 1 to 0, then back to 1 (so called “break in interaural correlation”, BIC). Note that introducing a BIC does not significantly alter monaural inputs. Until now, the neural correlates of the BIC in the central auditory system have not been reported in the literature.

The peripheral auditory system not only bandpass-filters broadband sounds into a series of narrowband waves orderly distributing along the basilar membrane, but also decomposes narrowband waves into both quickly-varying temporal fine structures (TFSs) and slowly-varying envelopes (Moore, 2008; Rosen, 1992). These two temporal components are subsequently represented by temporal firing patterns of the auditory nerves (Johnson, 1980;
Joris and Yin, 1992; Young and Sachs, 1979). Although the neural representation of a BIC in the central auditory system may contain TFS and envelope components, listeners in fact do not perceive the BIC as separated TFS and envelope percepts.

Both scalp-recorded and intracranially recorded frequency-following responses (FFRs) are sustained neuro-electrical potentials based on precisely phase-locked responses of neuron populations to instantaneous waveforms of low-to-middle-frequency acoustic stimuli (Chandrasekaran and Kraus, 2010; Du et al., 2009a, b, 2011; 2012; Marsh and Worden, 1969; Moushegian et al., 1973; Ping et al., 2008; Weinberger et al., 1970; Worden and Marsh, 1968). FFRs can efficiently convey both TFS information (e.g., Chandrasekaran and Kraus, 2010; Du et al., 2011; Galbraith, 1994; Krishnan, 2002; Krishnan and Gandour, 2009; Russo et al., 2004) and envelope information (also called envelope-following response) (e.g., Aiken and Picton, 2006, 2008; Dolphin and Mountain, 1992, 1993; Hall, 1979; Shinn-Cunningham et al., 2013; Supin and Popov, 1995; Zhu et al., 2013). FFRs start to occur in the auditory nerve (Dau, 2003) and can be intracranially recorded in both the lower auditory brainstem structures (Kuokkanen et al., 2010; Wagner et al., 2005, 2009) and the auditory midbrain, the inferior colliculus (IC, Du et al., 2009b; Ping et al., 2008). In humans, the origin of human scalp-recorded FFRs has been widely considered as the IC (e.g., Chandrasekaran and Kraus, 2010; Marsh, 1974; Smith et al, 1975; Sohmer et al, 1977; Weinberger et al., 1970).

The IC is the endpoint that both converges inputs from lower auditory brainstem structures and processes IAC signals (Yin et al., 1987; Palmer et al., 1999; Shackleton et al., 2005; Shackleton and Palmer, 2006). It is also considered as the critical generator for human
scalp-recorded FFRs (Chandrasekaran and Kraus, 2010; Marsh, 1974; Smith et al, 1975; Sohmer et al, 1977; Weinberger et al., 1970). This study was to investigate the following four issues using rats as the mammal modeling subjects: (1) In the IC, whether a narrowband noise can evoke local-field FFRs that contain the TFS component (FFR_TFS) and the envelope component (FFR_Env), (2) whether the FFR_TFS and/or FFR_Env to interaurally correlated noises are affected by introducing a BIC, (3) whether the BIC-evoked change in FFR_TFS contributes to the neural BIC detection differently from that in FFR_Env, and (4) whether the binaural integration of IC neuron populations for neural detection of a BIC is based on a simple linear summation (i.e. cross-correlation) of noise signals from the two ears.
MATERIALS AND METHODS

Animal Preparation

Eight younger-adult male Sprague-Dawley rats (age: 10-12 weeks; weight: 280-350 grams) were purchased from the Vital River Experimental Animal Company. They were anesthetized with 10% chloral hydrate (400 mg/kg, intraperitoneal) and the state of anesthesia was maintained throughout the experiment by supplemental injection of the same anesthetic. Stainless-steel recording electrodes (10-20 kΩ) insulated by a silicon tube (0.3 mm in diameter) except at the 0.25 mm diameter tip (Du et al., 2009b; Ping et a., 2008) were aimed at the central nucleus of the IC bilaterally. Based on the stereotaxic coordinates of Paxinos and Watson (1997) and referenced to Bregma, the coordinates of the aimed IC site were: AP, -8.8 mm; ML, ±1.5 mm; DV, -4.5 to -5.0 mm. Two electrodes were inserted per animal, one on each side of the IC.

Rats used in this study were treated in accordance with the Guidelines of the Beijing Laboratory Animal Center, and the Policies on the Use of Animal and Humans in Neuroscience Research approved by the Society for Neuroscience (2006). The experimental procedures were also approved by the Committee for Protecting Human and Animal Subjects in the Department of Psychology at Peking University.
Apparatus and Stimuli

All the sound waves were processed by a TDT System II (Tucker-Davis Technologies, FL, USA) and presented through two ED1 earphones. Two 12-cm TDT sound-delivery rubber tubes were connected to the ED1 earphones and inserted into each of the rat’s ear canals for sound delivery. All the narrow-band noises were calibrated using a Larson Davis Audiometer Calibration and Electroacoustic Testing System (AUDitTM and System 824, Larson Davis, USA). The sound pressure level (SPL) of all signals was 72 dB for each earphone.

Gaussian wideband noises (10-kHz sampling rate, and 16-bit amplitude quantization) were generated, and filtered by a 512 point digital filter with the center frequency of 2000 Hz and the bandwidth of 0.466 octaves using MATLAB (the MathWorks, Natick, MA, U.S.A.). All the stimulus duration was 900 ms with 10-ms linear onset/offset ramps and the (offset-onset) inter-stimulus interval was 100 ms.

Under the baseline-stimulation condition that occurred before and after the occurrence of either the BIC or the interaurally correlated amplitude gap (Corgap), the interaurally correlated noises (IAC = 1) were presented with the total duration of 900 msec. Under the BIC-stimulation condition, a 200-msec uncorrelated noise fragment (IAC = -0.046) were substituted into the temporal middle of the noise (i.e., from 350 to 550 msec from the noise onset) with no interaural delays. Note that mathematically the amplitude of the linear summation of two uncorrelated noises is smaller than that of two correlated noises (Figure 1). Thus, if the central binaural integration followings the simple theoretical summation, the
magnitude of neural signals under the BIC-stimulation condition should be smaller than that
under the baseline-stimulation condition (Figure 1B, left panel).

Since the linear summation of binaural signals under the BIC-stimulation condition leads
to an amplitude reduction (Figure 1A), the Corgap-stimulation condition was introduced as
the stimulation control condition. Under the Corgap-stimulation condition, the two
monaurally presented noises were identical (correlated), but their amplitudes were equal to
50% of the left-right summated signal amplitude under the BIC-stimulation condition. In
other words, the linearly summed left-ear and right-ear signals the under the
BIC-stimulation condition and that under the Corgap-stimulation condition are identical
(Figure 1). The BIC and Corgap were distinguished in the value of the IAC coefficient
(during the fragment period from 350 to 550 msec after the sound onset). Note that
monaurally the intensity of the Corgap-stimulation condition was reduced during the
fragment period compared to the pre- and post-fragment periods, but the monaural intensity
under the BIC-stimulation condition was not reduced.

Evoked neural potentials were recorded in a sound-attenuating chamber, amplified 1000
times by a TDT DB4 amplifier, filtered through a 100-10000 Hz band-pass filter (with a
50-Hz notch), and averaged 100 times per stimulation condition. Online recordings were
processed with TDT Biosig software, digitized at 16 kHz, and stored on a disk for off-line
analyses. The same stimuli were used for each animal under a certain stimulation condition. Also, both the pre-fragment and the post-fragment were not changed across stimulation conditions.

Data Analyses

Theoretically, a steady-state Gaussian narrowband noise with a center frequency of $c$ Hz and a bandwidth of $b$ Hz has the TFS energy around $c$ Hz and the envelope energy within the frequency range between 0 and $b$ Hz (Longtin et al., 2008). Thus, for a narrowband noise with bandwidth $b$, the TFS energy distributes from the low-cut ($f_{lc}$) to the high-cut ($f_{hc}$) frequencies, and the $f_{hc}$ is below the frequency $b$. The normalized amplitude of $\text{FFR}_{\text{TFS}}$ can be calculated by the following function:

$$\text{FFR}_{\text{TFS}}_{\text{normalized amplitude}} = \frac{\sum_{i=f_{lc}}^{f_{hc}} \text{Amp}_n}{\sum_{n=2}^{5000}}$$  

(1)

The normalized amplitude of $\text{FFR}_{\text{Env}}$ can be calculated by the following function:

$$\text{FFR}_{\text{Env}}_{\text{normalized amplitude}} = \frac{\sum_{i=2}^{b} \text{Amp}_n}{\sum_{n=2}^{5000}}$$  

(2)

where the denominator represents the level of noise floor ranging from 2 to 5000 Hz while the numerator represents the spectral region of interest. The $\text{FFR}_{\text{TFS}}$ and $\text{FFR}_{\text{Env}}$ components were extracted to calculated normalized amplitude using Functions 1 and 2.

To estimate the neural detection of the BIC fragment and that of the Corgap fragment,
responses in each of the three 200-ms periods were separately processed: pre-fragment (100-300 msec after the noise onset), fragment (350-550 msec), and post-fragment (600-800 msec). Furthermore, the (neural) fragment detection index (FDI) was defined as the relative difference between the amplitude of the fragment (BIC or Corgap) and the average of pre-fragment amplitude and post-fragment amplitude (normalized against the average of pre- and post-fragment amplitudes).

Statistical Analyses

Statistical analyses were performed with IBM SPSS Statistics 20 (SPSS Inc., Chicago, Illinois 60606). Within-subjects, repeated-measures analyses of variance (ANOVAs), t-tests, and Pearson correlation were conducted to examine differences between stimulation conditions or correlation between responses. The null-hypothesis rejection level was set at 0.05.

Histology

When all recordings were completed, rats were euthanized with an overdose of chloral hydrate. Lesion marks were made via the recording electrodes with an anodal DC current (500 μA for 10 s). The brains were stored in 10% formalin with 30% sucrose and then sectioned at 55 μm in the frontal plane in a cryostat (-20℃). Sections were examined to
determine locations of recording electrodes.

RESULTS

Histological Results and Response Latencies

According to the histological examination, all the 16 electrodes were located precisely within the central nucleus of IC in all rats (Figure 2A). Each of the electrodes was used in experimental recordings. The response latency to the noise-stimulus onset was examined by cross-correlation analyses of the best delay between the noise-stimulus waveform and the evoked neural response waveform (Burkard, 1991; Dobie and Wilson, 1984). The best delay, at which the stimulus-response correlation reached the maximus, was ranged from 5.8 to 6.1 msec with the mean of 6.0 msec, in consistent with the results reported by previous studies (Du et al., 2011; Ping et al., 2008).

To estimate whether there exist binaural sluggishness in IC FFRs, the latency of IC FFR to the BIC was compared to that to the Corgap using cross-correlation analyses of the best delay between the fragment waveform (350-550 msec after sound onset) and the evoked neural response waveform. Pairewise t-test showed that there was no significant difference between the latency for BIC (mean = 5.99, SD = 0.35) and that for Corgap (mean = 6.01, SD = 0.39) [t (13) = -0.034, p = 0.974]. The results suggested that there was no binaural sluggishness at the
midbrain level (also see Fitzpatrick et al., 2009).

Effects of the BIC or Corgap on \( \text{FFR}_{\text{TFS}} \) and \( \text{FFR}_{\text{Env}} \)

The results of this study clearly showed that narrowband noises could evoke FFRs containing both the \( \text{FFR}_{\text{TFS}} \) and \( \text{FFR}_{\text{Env}} \) components under each of the stimulation conditions (the baseline, BIC, and Corgap, see Figure 2B for examples of the BIC- and Corgap-stimulation conditions).

The narrowband noise used in this study had the TFS energy around 2000 Hz (center frequency) and the envelope energy within the frequency range between 0 and 640 Hz (bandwidth). As the example shown in Figure 2B (bottom panels), the fragment-induced \( \text{FFR}_{\text{TFS}} \) and \( \text{FFR}_{\text{Env}} \) exhibited the similar spectra with the stimulus TFS and envelope, respectively (see Longtin et al., 2008).

To examine how faithful the \( \text{FFR}_{\text{TFS}} \) and \( \text{FFR}_{\text{Env}} \) were in representing acoustic features of the noise stimulus, the significance of the stimulus-to-response (S-R) correlation for the pre-fragment noise section (100-300 msec after sound onset) was examined at each recording site using Pearson correlation tests. The results showed that the S-R correlation between the noise-stimulus TFS and the IC \( \text{FFR}_{\text{TFS}} \) was significant (for all recording sites, \( p < 0.05 \)); the S-R correlation between the noise envelope and IC \( \text{FFR}_{\text{Env}} \) was also significant (for all recording sites, \( p < 0.001 \)).

To examine whether the BIC and Corgap fragments affected IC FFRs, normalized amplitudes of \( \text{FFR}_{\text{TFS}} \) and \( \text{FFR}_{\text{Env}} \) in the three periods (pre-fragment, fragment, and
post-fragment) were calculated separately. Figure 3A shows that both $FFR_{TFS}$ and $FFR_{Env}$ decreased as either the BIC or Corgap occurred. For the $FFR_{TFS}$, a two-by-three (stimulation condition: BIC, Corgap; response period: pre-fragment, fragment, and post-fragment) two-way repeated-measured-ANOVA showed that the both the main effect of stimulation condition [$F_{1,15} = 8.889, p = 0.009, \text{partial } \eta^2 = 0.372$] and the main effect of response period [$F_{1,15} = 22.249, p < 0.001, \text{partial } \eta^2 = 0.597$] were significant, but the interaction effect was not significant [$F_{2,30} = 0.606, p = 0.552, \text{partial } \eta^2 = 0.039$]. Post hoc tests confirmed that the amplitude of $FFR_{TFS}$ during the BIC was significantly lower than that during the Corgap ($p = 0.031$, with Bonferroni adjustment).

For $FFR_{Env}$, a two-way repeated-measured-ANOVA showed that the both the main effect of stimulation condition [$F_{1,15} = 5.563, p = 0.032, \text{partial } \eta^2 = 0.271$] and the main effect of response period [$F_{1,15} = 17.629, p < 0.001, \text{partial } \eta^2 = 0.540$] were significant, but the interaction between the two factors was not significant [$F_{2,30} = 2.122, p = 0.137, \text{partial } \eta^2 = 0.124$]. Post hoc tests confirmed that the amplitude of $FFR_{Env}$ during the BIC was significantly lower than that during the Corgap ($p = 0.040$, with Bonferroni adjustment).

Post hoc tests also showed that no significant differences occurred between the pre- and post- fragments under each of the stimulation conditions (for all $p > 0.05$, with Bonferroni adjustment). Thus, the normalized amplitudes of pre- and post-fragments were averaged in the following analyses of the fragment effects.

------ Insert Figure 3 about here ------
Correlations between Fragment Detection Indices

The fragment detection index (FDI) was introduced as the relative amplitude difference between FFRs during the fragment and the average of pre- and post-fragment FFRs (details see Materials and Methods). To test whether the FDI under the BIC-stimulation condition and that under the Corgap-stimulation condition shared a common neural mechanism, Pearson correlation tests for FDI between the two conditions were conducted for $\text{FFR}_\text{TFS}$ and $\text{FFR}_\text{Env}$, separately. As shown in Figure 3B, no significant correlation was found between the two stimulation conditions for either $\text{FFR}_\text{TFS}$ or $\text{FFR}_\text{Env}$.

To compare the effect of introducing a BIC or Corgap on the $\text{FFR}_\text{TFS}$ and that on the $\text{FFR}_\text{Env}$, the $\text{FFR}_\text{TFS}$-$\text{FFR}_\text{Env}$ FDI matrix was examined, in which $\text{FFR}_\text{TFS}$ was presented in $y$-axis and $\text{FFR}_\text{Env}$ was presented in $x$-axis (Figure 4). As shown in Figure 4, the majority of the BIC $\text{FFR}_\text{TFS}$ FDIs was larger than the BIC $\text{FFR}_\text{Env}$ FDIs (most filled circles are above the diagonal). However, this pattern was not present for Corgap FDIs.

DISCUSSION

This study showed that a steady-state narrowband noise can elicit remarkable FFRs in
the auditory midbrain IC, which is the endpoint integrating inputs from lower auditory brainstem structures for binaural processing (Li et al., 1992; Yin et al., 1987; Palmer et al., 1999; Shackleton et al., 2005; Shackleton and Palmer, 2006). Since FFRs are based on precisely phase-locked responses of neuron populations to instantaneous waveforms of acoustic stimuli (Chandrasekaran and Kraus, 2010; Du et al., 2009a, b, 2011; 2012; Marsh and Worden, 1969; Moushegian et al., 1973; Ping et al., 2008; Weinberger et al., 1970; Worden and Marsh, 1968), narrowband noises are useful for investigating phase-locking based neural mechanisms underlying binaural integration.

Moreover, the noise-evoked FFRs exhibit two temporal components: the fast-varying $\text{FFR}_{\text{TFS}}$ signaling the center frequency and the slowly-varying $\text{FFR}_{\text{Env}}$ signaling the bandwidth. Thus, the $\text{FFR}_{\text{TFS}}$ and $\text{FFR}_{\text{Env}}$ precisely represent the spectral features of a narrowband noise. The results support that FFRs efficiently convey both TFS information (e.g., Chandrasekaran and Kraus, 2010; Du et al., 2011; Galbraith, 1994; Krishnan, 2002; Krishnan and Gandour, 2009; Russo et al., 2004) and envelope information (also called envelope-following response) (e.g., Aiken and Picton, 2006, 2008; Dolphin and Mountain, 1992, 1993; Hall, 1979; Shinn-Cunningham et al., 2013; Supin and Popov, 1995; Zhu et al., 2013).

More importantly, this study for the first time provides evidence showing that introducing a BIC reduces both the $\text{FFR}_{\text{TFS}}$ and $\text{FFR}_{\text{Env}}$. Since introducing a BIC does not substantially change monaural inputs, the FFR reduction must be based on binaural interactions, which have been demonstrated previously (Du et al., 2009b). The BIC-induced
FFR reduction may be the neural correlate underlying perceptual detection of the BIC (Akeroyd and Summerfield, 1999; Boehnke et al., 2002; Huang et al., 2008, 2009a,b; Kong et al., 2012, 2015; Li et al., 2009; Li et al., 2013).

When the FDI is used to estimate the degree of FFR changes caused by introducing a fragment (BIC or Corgap), the BIC-induced FDI for $FFR_{TFS}$ is larger than that for $FFR_{Env}$, indicating that introducing a BIC cause more reduction in $FFR_{TFS}$ than that in $FFR_{Env}$. The Boehnke et al. study (2002) has shown that the envelope information is not as important as the TFS information in determining the detection of the BIC detection. Clearly, further perceptual work is needed to verifying whether the processing of $FFR_{TFS}$ contributes more to the BIC detection than the processing of $FFR_{Env}$. However, the Corgap-induced FDI for $FFR_{TFS}$ is not significantly different from that for $FFR_{Env}$. Since the IAC-based binaural processing plays a role in both sound localization (Coffey et al., 2006; Franken et al., 2014; Soeta and Nakagawa, 2006) and target-object detection against masking (Durlach et al., 1986; Palmer et al., 1999), further perceptual work is also needed to verify whether $FFR_{TFS}$ signals are more involved in sound localization and target unmasking than $FFR_{Env}$ signals. Smith et al. (2002) have suggested that TFS signals and envelope signals are most important for pitch/location perception and speech recognition, respectively. It is of interest to know whether this functional dichotomy between TFS and envelope is associated with certain differences in sensitivity to the BIC between $FFR_{TFS}$ and $FFR_{Env}$.

The IC is the endpoint converging inputs from lower auditory brainstem structures (Yin et al., 1987; Palmer et al., 1999; Shackleton et al., 2005; Shackleton and Palmer, 2006).
Previous studies have suggested that binaural integration occurs in the IC (Kelly and Li, 1997; Li et al., 1992; Du et al., 2009b). Does the IAC-based binaural integration follow a simple linear summation (cross-correlation) function? The results of this study indicate that for either FFR_{TFS} or FFR_{Env}, the BIC-induced FDI is independent to the Corgap-induced FDI. Thus, the BIC-induced changes in FFRs cannot be explained by a simple signal-input reduction.

**SUMMARY**

In the IC, a narrowband noise can efficiently induce FFRs that contain both the FFR_{TFS} and FFR_{Env} components, signaling the center frequency and bandwidth, respectively. Introducing a BIC reduces both FFR_{TFS} and FFR_{Env}, and the FFR reductions cannot be explained by a simple reduction in linear summation of signal inputs from the two ears.
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FIGURE LEGENDS

Figure 1. Panel A: Waveforms of the monaural noise stimuli and the theoretically linearly summated waveforms of the monaural stimuli. Under the condition of break in interaural correlation (BIC), a 200 msec uncorrelated noise pair was substituted into the temporal middle (350 to 550 msec from the onset) of the noise stimuli. Under the condition of interaurally correlated amplitude-gap (Corgap), the two monaurally presented noises were identical (correlated), but their amplitudes were individually equal to 50% of the left-right summated signal amplitude under the BIC-stimulation condition. Bottom Panels: Comparisons in normalized amplitude between the baseline-stimulation condition (pre- and post-fragment), the BIC-stimulation condition, and the Corgap-stimulation condition. Note that under the Corgap-stimulation condition, the amplitude of the noise at each ear was so reduced that the linear summation of the noises from the two ears led to the noise signal identical to the one after the linear summation the noises from the two ears under the BIC-stimulation condition.

Figure 2. Panel A: Histological results of recording electrodes in 8 rats. Electrodes were precisely located within the central nucleus of the inferior colliculus (IC) in 16 of the 16 penetrations (filled circles and the star). Note that two electrodes were inserted per animal, one on each side of the IC. Panel B: Frequency-following responses (FFRs) recorded from a randomly selected recording site (the star) to the BIC (left subpanels) or the Corgap (right subpanels).
The FFRs contained two components (FFR_{TFS} and FFR_{Env}) signaling the stimulus temporal fine structure (TFS) and envelope, respectively.

Figure 3. Panel A: Comparisons in normalized FFR amplitude across stimulation conditions for the FFR_{TFS} (left panel) and the FFR_{Env} (right panel). White bars, the fragment period, 350-550 msec after the sound onset. Stripped bars, pre-fragment period, 100-300 msec after the sound onset. Black bars, post-fragment period, 600-800 msec after the sound onset. Error bars: Standard errors of the mean. *, $p < 0.05$; **, $p < 0.01$.

Panel B: Examinations of the correlation in the neural fragment-detection index (FDI) between the BIC-stimulation condition and the Corgap-stimulation condition for the FFR_{TFS} (left panel) and the FFR_{Env} (right panel).

Figure 4. Examination of the correlation in FDI between the FFR_{TFS} and the FFR_{Env} under the BIC-stimulation condition and that under the Corgap-stimulation condition. Note that under the BIC-stimulation condition, most of the FFR_{TFS} FDIs were larger than FFR_{Env} FDIs (black dots), and the FFR_{TFS} FDI was significantly correlated with the FFR_{Env} FDI. However, under the Corgap-stimulation condition (open dots), the FFR_{TFS} FDI was not correlated with the FFR_{Env} FDI. Triangle: the mean of the BIC FDIs; rectangular: the mean of the Corgap FDIs. Solid line: linear regression for the BIC data. Broken line: linear regression for the Corgap data. Error bars: Standard errors of the mean. **, $p < 0.01$. 
A  

**LEFT EAR**  

**RIGHT EAr**  

**LINEAR SUMMATION**

* **BIC:** break in interaural correlation*

![Waveform plots showing BIC](image)

* **Corgap:** interaurally correlated energy gap*

![Waveform plots showing Corgap](image)

B  

**BIC**  

**CORGAP**

![Histograms showing BIC and Corgap](image)

**Summation Conditions**
A

-8.8 mm

-9.2 mm

B

**BIC**

**CORGAP**

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<tr>
<td>0</td>
</tr>
<tr>
<td>2</td>
</tr>
<tr>
<td>4</td>
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</tbody>
</table>

**FFR**

**Env**

**FFR_{TFS}**

-8.8 mm

-9.2 mm
**A**

![FFR TFS and FFR Env graphs](image)

- **FFR TFS**
  - Pre-fragment
  - Fragment
  - Post-fragment

- **FFR Env**
  - Pre-fragment
  - Fragment
  - Post-fragment

**B**

![FFR TFS and FFR Env correlation graphs](image)

- **FFR TFS**
  - Correlation: $r = 0.201$, $p = 0.456$

- **FFR Env**
  - Correlation: $r = 0.176$, $p = 0.515$
A scatter plot showing the relationship between Fragment Detection Index (FFR$_{TFS}$) and Fragment Detection Index (FFR$_{Env}$). The plot includes data points for BIC (solid circles) and Corgap (open circles). The relationship appears to be linear, with a dashed line indicating the trend. The x-axis represents FFR$_{Env}$, ranging from 0 to 1.5, and the y-axis represents FFR$_{TFS}$, also ranging from 0 to 1.5. The plot includes statistical significance markers, represented by asterisks (**).